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One more new bent-toed gecko of the Javanese *Cyrtodactylus marmoratus* complex (Squamata: Gekkonidae) from East Java, Indonesia

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Abstract

Here, we describe a new species of *Cyrtodactylus* Gray from East Java (Dampit, Malang), Indonesia that belongs to the *C. marmoratus* species group. It is a medium-sized (SVL) species with adult males reaching 65.9 mm in males, 64.3 mm in females; characterized by dorsal tubercle absent on brachium, 17–18 dorsal tubercle rows, 38–40 rows of smooth ventrals, precloacal depression present in a deep groove, 15–17 precloacal pores in an inverse Y shape, 7–12 femoral pores, 3–5 poreless femoral scale separated precloacal and femoral pores in males, 2 pairs of post caudal tubercles, second post mentals separated by 5–7 scales, abrupt transition between rows of large and small postfemoral and ventral femoral scales, and no enlarged subcaudals. The new species is genetically divergent from the other Javan congeners of the *C. marmoratus* complex with genetic divergences (p-distances) ranging from 15.1–24.3% for the mitochondrial ND2 gene. This description brings the number of nominal species of bent-toed gecko in Java to six.

Key words: *darmandvillei, marmoratus, new species, Java, taxonomy*

Introduction

Currently, there are five described bent-toed geckos of the genus *Cyrtodactylus* Gray known to occur on Java Island: *C. marmoratus* Gray, 1831, *C. semiadii* Riyanto, Bauer & Yudha, 2014, *C. petani* Riyanto, Grismer & Wood, 2015a, *C. belanegara* Riyanto, Hikmah, Amarasinghe, Abinawanto & Hamidy, 2024a, and *C. pecelmadiun* Riyanto, Sidik, Hamidy, Grismer & Abinawanto, 2025. Those species belong to the *marmoratus* group and the *darmandvillei* group. Riyanto *et al.* (2024) revealed that *C. belanegara*, *C. marmoratus*, and *C. semiadii* belong to *marmoratus* group (*sensu* Grismer *et al*. 2021), meanwhile Riyanto *et al.* (2025) revealed that *C. pecelmadiun* and *C. petani* placed in *darmanvillei* group (*sensu* Grismer et al. 2021) and belong to *sadleiri* complex (sensu Reilly *et al*. 2023).

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A morphological study on the Javanese population of *Cyrtodactylus marmoratus* has revealed variation (Wiradarma *et al.* 2019). The *C. marmoratus* from Cibodas (West Java) clearly differs from other specimens identified as *C. marmoratus* originally from Sumatra and Borneo (Fauzi *et al.* 2024). The taxonomic status of *Cyrtodactylus* in Java has inspired and encouraged further studies using integrative taxonomy methods with an adequate sample from a broader range of localities. In this paper, we describe a new species, which is one of the results of our research on the taxonomic status of Javanese *Cyrtodactylus*.

Materials and Methods

Sampling. In September 2019, three of us (AR, MAF, and AMK) conducted a brief field trip in Lumajang and Dampit (East Java), and collected four *Cyrtodactylus* specimens from hillside fields in Dampit, which have a topography ranging in elevation from 400 to 500 meters above sea level. All specimens were euthanized with sodium pentobarbital, and fixed in 10% buffered formalin prior to storage in 70% ethanol. The liver tissue samples were preserved for DNA analysis in 95% ethanol. All specimens were permanently deposited at the Museum Zoologicum Bogorienese (MZB), National Research and Innovation Agency, Cibinong, West Java, Indonesia.

Molecular analyses. We followed Riyanto *et al*. (2020) and considered DNA sequences from specimens from Cibodas, West Java to represent true *C. marmoratus* and used *Gekko gecko* and *Hemidactylus frenatus* as outgroups. The genomic DNA from liver samples was extracted using a Qiagen DNeasy Extraction Kit. A partial mitochondrial sequence of the protein-encoding gene NADH dehydrogenase subunit 2 (ND2) was amplified with the primers following Oliver *et al*. (2016) M112F (5'–AAGCTTTCGGGGCCCATACC–3') and M1123R (5'–GCTTAATTAAAGTGTYTGAGTTGC–3'). The PCRs were performed in 25 µL total volumes using Top Taq by Qiagen comprising 1.0 µL DNA template, 2.5 µL 10X Top Taq PCR buffer, 0.5 µL 10mM dNTP mix, 2.5 µL 10X CoralLoad, 5 µL 5X Q solution, 1.0 µL light strand primer, 1.0 µL heavy strand primer, 0.125 µL Top Taq DNA polymerase with appropriate buffer and ddH$_2$O to volume. PCR reactions were executed on an Eppendorf Mastercycler under the following conditions: initial denaturation at 94^{o}C for 9 min, second denaturation at 94^{o}C for 45 s, annealing at 60^{o}C for 45 s, and a cycle extension at 72^{o}C for 1 min, for 35 cycles. Purified PCR products were sequenced by 1st Base Asia, Singapore. New genetic sequences generated in this work were deposited in GenBank.

DNA sequences and available data from GenBank (Appendix 1) were assembled and aligned using Clustal W in MEGA X v10.1.7 (Kumar *et al*. 2018). The uncorrected *p*-distance (sequence divergence) was calculated in MEGA X, and all ambiguous positions were removed for each sequence pair (pairwise deletion option employed). The final alignment of ~ 1010 bp was analysed using Maximum Likelihood (ML), implemented in IQ-TREE (Nguyen *et al.* 2015). A total of 5000 bootstrap replications was run by using the ultrafast bootstrap method (Hoang *et al.* 2017). The TIM+F+I+G4 model was identified as the best fit using the IQ-TREE model test.

Morphological data. Measurements and scale counts were made on the right side of each specimen (except on labials and if damaged) under an AmScope dissecting microscope. Measurements were done by using a Mitutoyo digital calliper to the nearest 0.1 mm. The following measurement definitions were followed: snout–vent length (SVL), tip of snout to vent; tail length (TailL), vent to tip of tail; head length (HL), tip of snout to posterior edge of retroarticular process of lower jaw; head width (HW), straight line between angles of jaw; head height (HH), maximum height of head between occiput and throat; snout length (SL), tip of snout to anteriormost edge of orbit; eye to ear distance (EE), edge of orbit to anterior edge of ear opening; ear length (EL), maximum length of ear opening; orbit diameter (OD), horizontal diameter of orbit; rostral width (RW), straight line between border of the rostral scale with the first supralabials on the left and right sides; rostral height (RH), maximum height of rostral from the lower boundary to the upper part of the rostral bordering with post rostral scale; mental width (MW), the maximum width between the border of the mental with first infralabials; mental height (MH), the longest distance from the center of anterior the mental to the anterior contact point between the first postmentals; forearm length (ForL), taken on the ventral surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; axilla groin length (AGL), axilla to groin; tibia length (TibL), taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of the heel.

Following Riyanto *et al*. (2022), we counted supralabial scales from the first scale behind the rostral scale to the largest scale immediately posterior to dorsal inflection of posterior portion of upper jaw; infralabial scales (number of labial scales of lower jaw, beginning with first scale bordering mental shield, ending with last enlarged scale bordering angle of jaw); dorsal tubercles (DorT), number of longitudinal tubercle rows on dorsum at midbody between ventrolateral folds; paravertebral tubercles (PVT), tubercles along paravertebral region, counted between postaxial margin of arm and pre-axial margin of leg; ventral scales (VS), number of ventral scales at midbody, counted in one row between ventrolateral folds across the belly; number of lamellae under fingers 1–5 ($F_{1–5}$, subdigital lamellae counted from point where interdigital skin contacts digit regardless of condition of scales under digit at this point, including fractured scales but not the elongate ungual scale at the base of the claw [claw sheath] or lamellae that extend onto the palm at base of digit); number of lamellae under toes 1–5 ($T_{1–5}$, subdigital lamellae counted from point where interdigital skin contacts digit regardless of condition of scales under digit at this point, including fractured scales but not including the elongate ungual scale at the base of the claw or lamellae that extend onto plantar surface at the base of the digit). Basal subdigital scales were counted from the most proximal scale at least twice as large as adjacent palmar scales following Bauer *et al*. (2010). Where relevant we also noted the following characters: presence of tubercles on the dorsal surfaces of the upper arm (brachium), forearm (antebrachium) and thigh; presence of enlarged precloacofemoral scales (EPFS), and extent to which these formed a continuous series; and presence of transversely enlarged median subcaudals. An abrupt contact between large and small postfemoral scales and ventral femoral scales versus smooth transition evaluated by following Grismer *et al*. (2016). The morphology of precloacal depressions was described according to Mecke *et al*. (2016).

Sex was determined as male if (1) preserved specimens showed enlarged hemipenial pockets, and confirmed by (2) viewing the hemipenes via a small lateral incision made at the base of the tail. By following Amarasinghe *et al*. (2015) and Harvey *et al*. (2015), we applied the reversible stain methylene blue in 70% ethanol to examine smaller characters such as keeling in the ventrals. Color notes were taken from digital images of living specimens prior to preservation. Comparative specimens examined in this paper are listed in Appendix 2.

Statistical analyses. Statistical analyses were conducted using R (R Core Team, 2021). Due to small sample size, statistically informative tests could not be performed on separate sexes (Zar, 2010). Juveniles were excluded to avoid the bias of allometry for the statistical analysis. To remove potential effects of allometry in the morphometric characters, size was normalized using the following equation: $Xadj = \log(X)-\beta[\log(SVL)-\log(SVLmean)]$, where Xadj = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVLmean = overall average SVL of all populations (Thorpe 1975, 1983; Lleonart *et al*. 2000) in the package GroupStruct (Chan & Grismer 2022). The morphometrics for each species were normalized separately and then concatenated so as not to conflate intra- with interspecific variation (Reist, 1986).

One-way ANOVA was run for Dampit population and described Javanese species to test means of these species, followed by Tukey's HSD test to know the differentiation each species on the significant characters. The significant differences in characters between these species are illustrated with box plots based on raw data. A multivariate analysis was conducted using Principal Component Analysis (PCA) on the scaled morphometrics above to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables [i.e., principal components (PC)]. The princomp function in the R statistical software program was used (v4.0.4; R Core Team 2021). Biplots of the first two principal component scores were used to examine the trajectory of the morphospatial differentiation between the species.

Results

The one-way ANOVA test revealed statistically significant differences among the four species for all morphometric characters measured. The degrees of freedom are 3 for among-group comparisons and 25 for within-group variation ($F_{(3,25)}$), indicating a total sample size of 29 individuals. The statistical results for each character are as follows: SVL ($F_{(3,25)} = 79.25$, $p = 6.66 \times 10^{-13}$), AGL.adj ($F_{(3,25)} = 197.4$, $p < 2 \times 10^{-16}$), HL.adj ($F_{(3,25)} = 272.5$, $p < 2 \times 10^{-16}$), HW.adj ($F_{(3,25)} = 138.6$, $p = 1.05 \times 10^{-15}$), HH.adj ($F_{(3,25)} = 138.6$, $p = 1.05 \times 10^{-15}$), SL.adj ($F_{(3,25)} = 158.8$, $p < 2 \times 10^{-16}$), OD ($F_{(3,25)} = 25.67$, $p = 8.39 \times 10^{-8}$), ForL ($F_{(3,25)} = 202.4$, $p < 2 \times 10^{-16}$), and TibL ($F_{(3,25)} = 278.2$, $p < 2 \times 10^{-16}$). Tukey's HSD post hoc test revealed statistically significant differences ($p \leq 0.05$) between the Dampit population and Javanese *C. marmoratus* species complex: from *C. marmoratus* in all assessed characters; from *C. belanegara* for the characters SVL, AGL, HL, HW, HH, ForL, and TibL; and from *C. semiadii* in all assessed characters (Table 1). Differences in morphometric characters among species are illustrated with box plots based on raw data

(Figure 1). The PCA analysis also showed distinct overall differences (Figure 2). PC1 captures the majority of the total variation (92.61%), with all morphological characters loading relatively equally and negatively on this axis (Table 2). This suggests that PC1 primarily reflects a general size gradient across variables. Given that allometric normalization was performed separately for each species, this indicates that species differences are driven more by overall body size than by variation in shape or proportion.

TABLE 1. Results of the Tukey post hoc test showing the *p*-values for all pairwise comparisons. Values highlighted in gray represent $p < 0.05$.

	mendol **sp.nov.**-*belanegara*	*mendol* **sp.nov.**-*marmoratus*	*semiadii*-*mendol* **sp.nov.**	*marmoratus* - *belanegara*	*semiadii* - *belanegara*	*semiadii* - *marmoratus*
SVL	0.0573844	0.0000000	0.4664566	0.0000000	0.0000940	0.0000000
AGL.adj	0.0000077	0.0000000	0.0000000	0.0000000	0.0007151	0.0000000
HL.adj	0.0000183	0.0000000	0.0000000	0.0000000	0.0000106	0.0000000
HW.adj	0.0000129	0.0000000	0.0000000	0.0000000	0.0000954	0.0000000
HH.adj	0.0000006	0.0000019	0.0000002	0.0000000	0.9686341	0.0000000
SL.adj	0.0606941	0.0000000	0.0000000	0.0000000	0.0000112	0.0000000
OD.adj	0.1989233	0.0043505	0.0401492	0.0000014	0.7962826	0.0000001
ForL.adj	0.0005386	0.0000000	0.0000000	0.0000000	0.0000784	0.0000000
TibL.adj	0.0000005	0.0000000	0.0000000	0.0000000	0.0000009	0.0000000

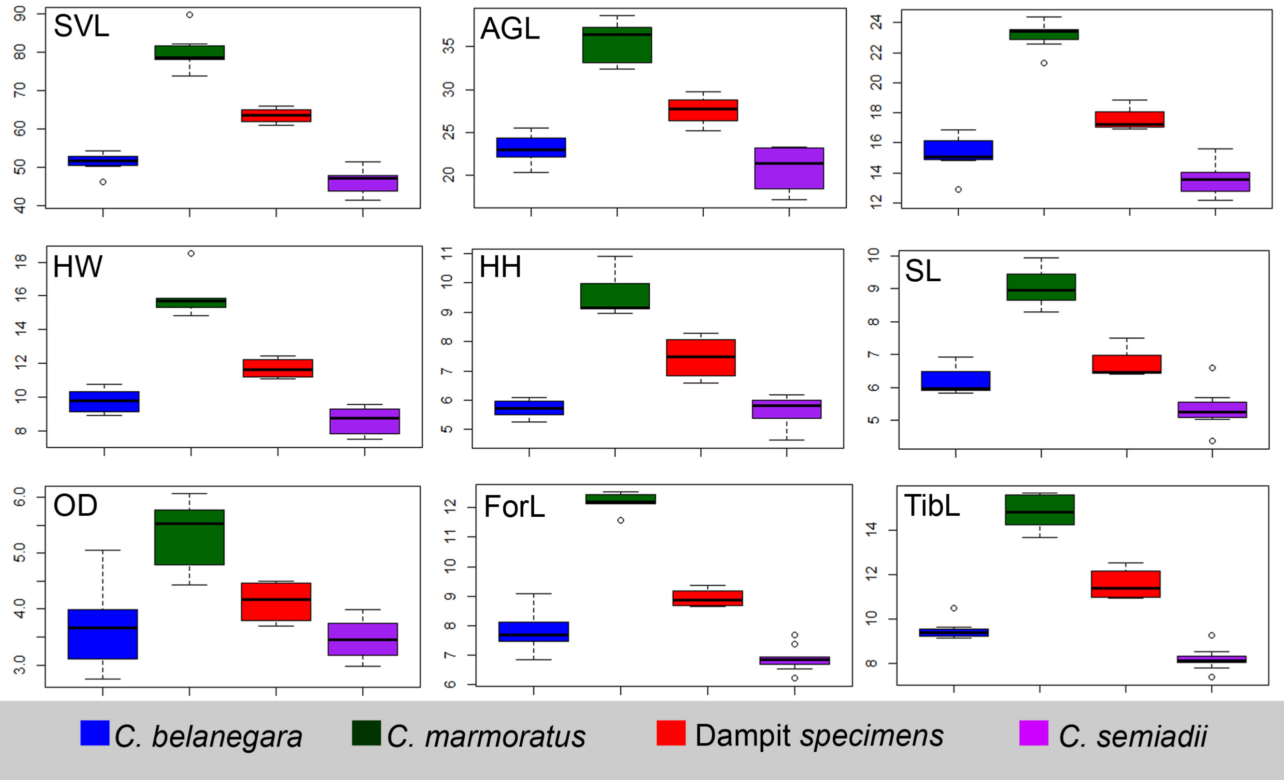

FIGURE 1. Box plots of nine adjusted morphometric characters illustrating the differences between specimens from Dampit and members of the Javanese *marmoratus* complex.

TABLE 2. Principal component analysis (PCA) and loadings. Principal component 1 (PC 1) and PC 2 collectively explained 95.29% of the variation.

PCA	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	2.8870	0.4915	0.4526	0.2900	0.2157	0.1747	0.1637	0.1403	0.1055
Proportion of variance	0.9261	0.0269	0.0228	0.0093	0.0052	0.0034	0.0030	0.0022	0.0012
Cumulative proportion (%)	92.61	95.29	97.57	98.50	99.02	99.36	99.66	99.88	100
Loadings									
SVL	-0.3095	0.8911	-0.1225	-0.2663	-0.0390	0.0275	-0.0864	-0.0405	0.1133
AGL.adj	-0.3380	-0.1752	-0.1537	0.0306	-0.8444	0.0506	-0.1648	0.2941	0.0370
HL.adj	-0.3410	-0.0455	-0.1299	0.1847	0.0468	-0.8603	-0.0537	-0.2312	-0.1791
HW.adj	-0.3418	-0.0931	-0.0383	-0.1049	-0.1050	0.1484	0.8591	-0.3011	-0.0148
HH.adj	-0.3306	-0.3542	-0.1024	-0.7856	0.2674	0.0208	-0.2086	0.0987	-0.1115
SL.adj	-0.3400	0.0519	-0.1900	0.3508	0.3775	0.1077	0.1720	0.6957	-0.2344
OD.adj	-0.3133	0.0286	0.9409	0.0154	-0.0088	-0.0438	-0.0321	0.1119	-0.0044
ForL.adj	-0.3418	-0.0482	-0.0501	0.3035	0.0720	0.4618	-0.3596	-0.4986	-0.4356
TibL.adj	-0.3420	-0.1824	-0.0934	0.2247	0.2303	0.0859	-0.1447	-0.1137	0.8345

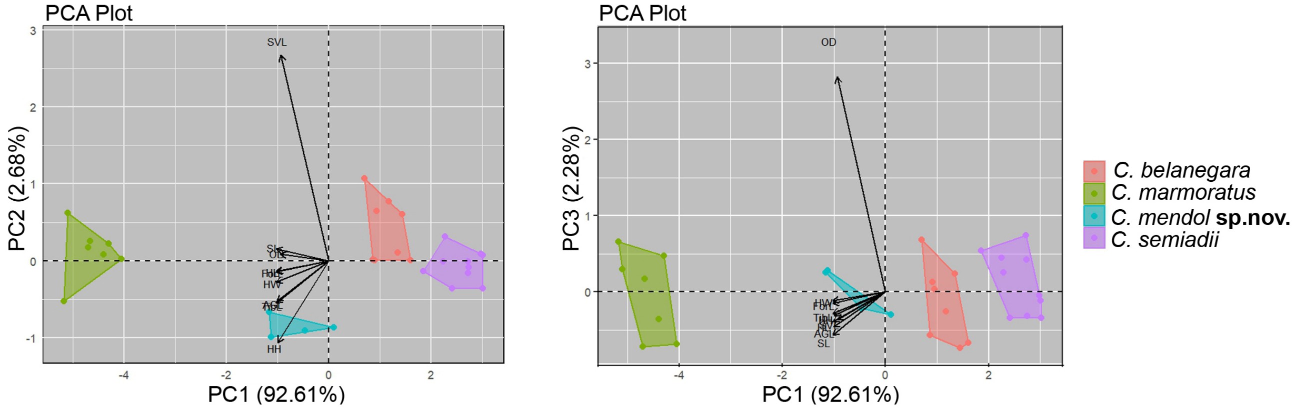

FIGURE 2. PCA plots illustrating the adjusted morphometric variation between specimens from Dampit and members of the Javanese *marmoratus* complex.

Our molecular analysis showed that the *Cyrtodactylus* specimens from Dampit (East Java) are nested within the *Cyrtodactylus marmoratus* group (sensu Grismer *et al*. 2021) with ultrafast support 98% (Figure 3). This lineage consists of lineage from Sundaland: Dampit population (East Java), *C. belanegara* (West Java), *C. marmoratus* (West Java), *C. semiadii* (Central and East Java), *C*. sp. 1 (southern Sumatra and West Java), *C*. sp. 2 (southern Sumatra and West Java), *C*. sp. 3 (West Java), and *C*. sp. 4 (Yogakarta), and sister lineage from Melanesia: *C. papuensis* (PNG), *C. papeda* (Obi Island), *C. papuensis, C.*cf. *papuensis* (Buru and Rajaampat Islands). The Dampit population is the sister taxon of *C*. sp. 4 specimen originally from Tanjungsari, Gunung Kidul (Yogakarta) with divergence in an uncorrected *p*-distance of 10.2–10.9%, and of *C. marmoratus* sensu stricto with genetic divergence 15.1–15.6%. Genetic divergence between the Dampit population and all other Javanese phylospecies in the *marmoratus* complex is high (range = 10.2–25.2%) (Table 3).

Given together the results of the molecular and morphological analyses demonstrate the Dampit population is strongly supported as a distinct species. Therefore, we describe it as a new species below.

TABLE 3. Uncorrected pairwise sequence divergence (%) for 1010 bp of the ND2 protein-coding mitochondrial gene among species of the *Cyrtodactylus marmoratus* group and *C. darmandvillei* group in Java. Sp. 1, 2, 3, and 4 refer to unnamed species.

	***C. mendol* sp. nov.**	***C. belanegara***	***C. marmoratus***	***C. semiadii***	**C. sp1**	**C. sp2**	**C. sp3**	**C. sp4**	***C. pecelmadiun***	***C. petani***
C. mendol **sp.nov.**	0.0–0.1									
C. belanegara	23.4–24.3	0.0								
C. marmoratus	15.1–15.6	21.3–22.0	0.1–3.2							
C. semiadii	21.3–22.1	21.8–22.6	20.2–21.2	0.7–4.8						
C.sp1	22.8–23.5	5.5–5.8	21.1–22.3	20.7–22.7	0.0–0.5					
C. sp2	23.6–25.2	11.7–11.8	21.0–21.7	19.5–20.7	11.1–11.5	0.5				
C. sp3	22.2–23.3	9.5–10.00	21.4–22.3	21.2–22.0	10.0	10.7–10.7	-			
C. sp4	10.2–10.9	22.9–23.1	13.9–14.9	21.3–22.7	22.4–23.1	22.1–22.2	22.3	-		
C. pecelmadiun	22.2–23.0	21.3–21.9	23.0–25.2	21.4–22.9	20.5–23.8	21.1–23.0	21.1–22.3	22.7–23.2	0.0–3.5	-
C. petani	20.7–21.8	22.1–22.4	21.3–21.9	20.2–20.7	20.7–23.4	21.8–22.5	21.6–22.1	22.7–22.9	8.6–9.9	0.1–1.5

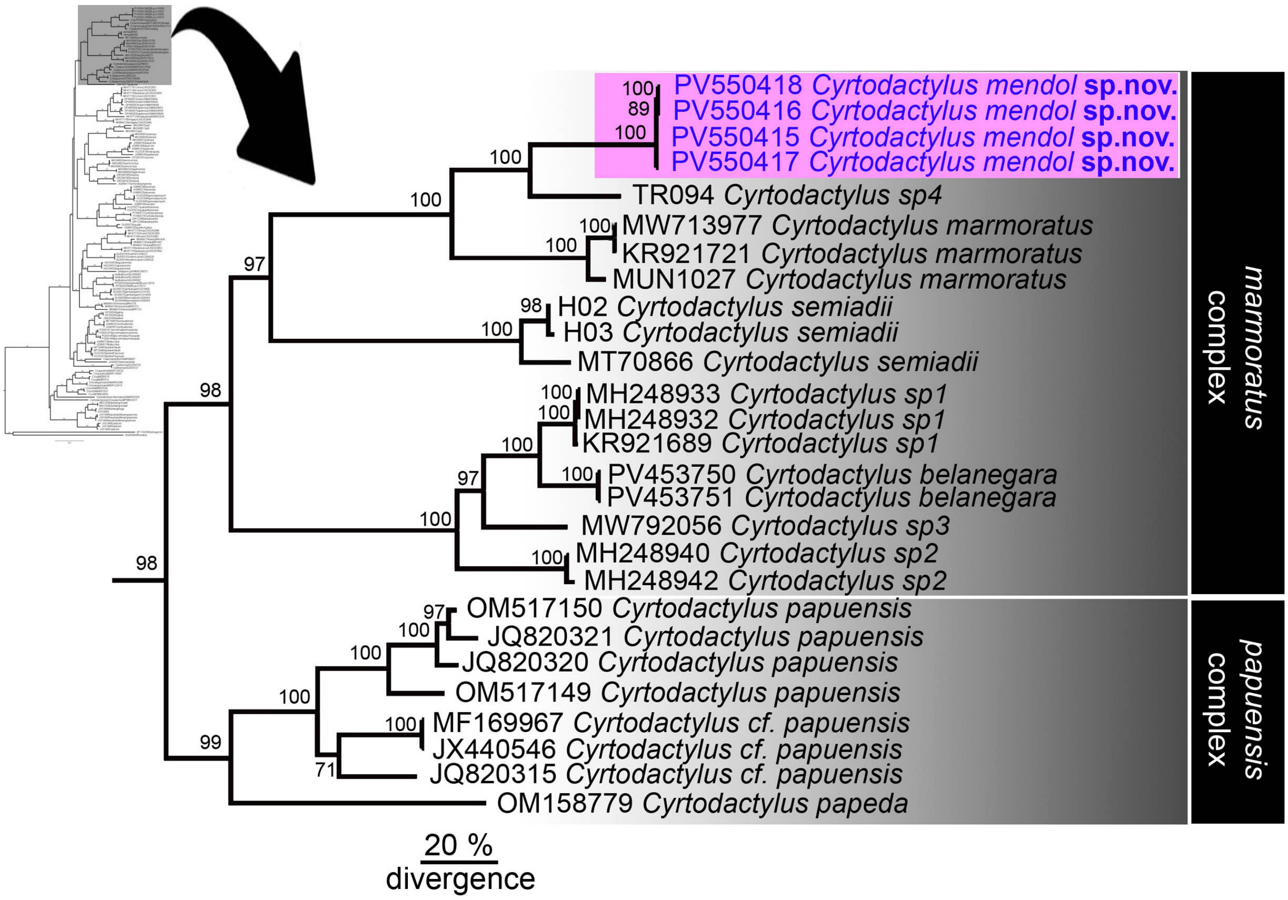

FIGURE 3. The phylogram from ML analysis showing the new species within the clade of *marmoratus* group using ~ 1010 bp fragment of ND2 mitochondrial gene and its flanking tRNAs.; outgroup taxa, *Gekko gecko* and *Hemidactylus frenatus*, are not shown.

Systematics

***Cyrtodactylus mendol* sp. nov.**
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Figs 4, 5
Mendol Bent-toed Gecko
Cecak jarilengkung Mendol

Holotype. Adult male (MZB.Lace.15007), from Polaman village, Dampit Regency, Malang District, East Java Province, Indonesia (8°14'37.2"S, 112°44'43.5"E, 448 m asl.), collected on 21 September 2019 by A. Riyanto, M.A. Fauzi and Ahmad M. Kadafi.

Paratypes. Adult male (MZB.Lace.15006), two females (MZB.Lace.15009–10), data as same holotype.

Diagnosis. The new species is a distinct evolutionary lineage closely related to *C. belanegara, C. marmoratus,* and *C. semiadii.* It can be differentiated from other congeners by the following combination of characters: known maximum SVL 65.9 mm in males, 64.3 mm in females; two pairs of post caudal tubercles; second post mentals separated by 5–7 scales; 17–18 dorsal tubercle rows; 30–35 paravertebral tubercles; 38–40 ventral smooth scales across midbody; precloacal depression, precloacal and femoral pores present in male; precloacal depression in a deep grooved form; 15–17 precloacal pores arranged in an inverted Y; 7–12 femoral pores; 3–5 poreless femoral scales separated from precloacal and femoral pores; abrupt transition between rows of large and small postfemoral and ventral femoral scales; absence of enlarged subcaudals.

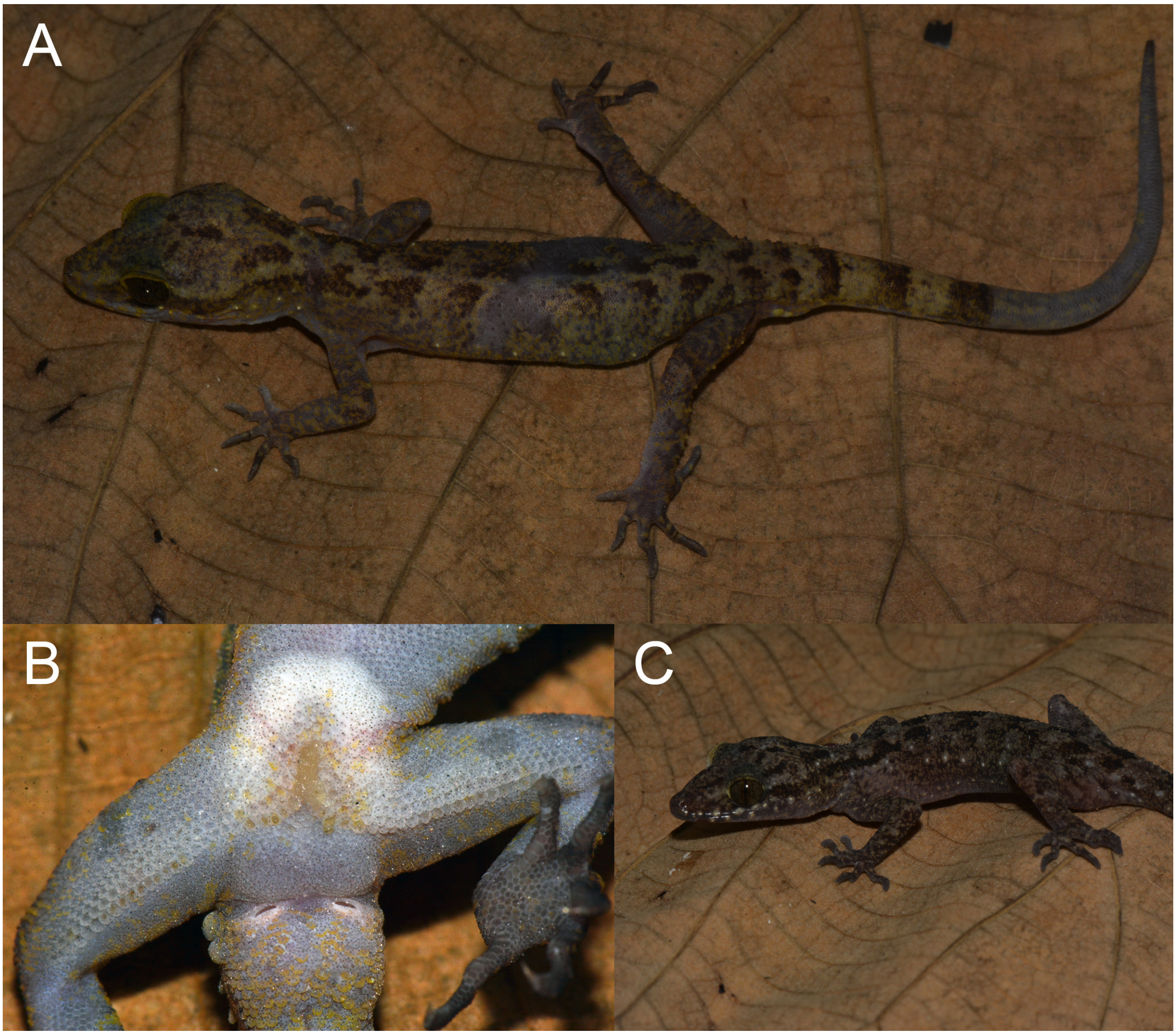

FIGURE 4. Living specimens of *Cyrtodactylus mendol* sp.nov., (A) adult male, MZBLace15007, holotype, (B) Precloacal region of the holotype, and (C) adult female, paratype, MZBLace15009. Photographs by: A. Riyanto.

Description of holotype. Moderate-sized species, male, 65.9 mm SVL; head triangular in dorsal view, distinct from neck; tubercles present on the occiput and dorsolateral sides of head; head long (HL/SVL 0.29), rather wide (HW/HL 0.66), head rather wider than high (HW/HH 1.50); snout elongate (SL/HL 0.40); canthus rostralis rounded, distance between eye-to-naris greater than the diameter of orbit (EE/OD 1.24); eye large (OD/HL 0.12); supraciliaries extending from anterior-ventral to posterior-dorsal edge of eye, longest at the anterior-dorsal part; ear opening small, dorsoventrally oblong, and oriented about 45 degrees to apex of rictus.

Rostral rectangular, incompletely divided dorsally by a Y-shaped shallow groove, wider than high (RW/RH 2.57), bordered posterolaterally by first supralabials and naris, and dorsally by five postrostral scales; naris oval, bordered anteriorly by rostral, anterodorsally by one postrostral, posteriorly by seven scales in right side and by seven scales in left side, and ventrally by first supralabials; orbit separated from supralabials by two rows of small lorilabial scales; 10 supralabial scales to angle of jaw in right side, 11 in left side; nine infralabial scales right side, 10 in left side. Mental triangular, slightly wider than long (ML/MW 0.76); bordered laterally by first infralabials, posteriorly by a pair of enlarged first postmentals, which contact medially over about 58.7% of their length; second postmentals ovoid, about one-third of the first postmentals and separated from each another by five granular scales; gular scales small, granular, grading to slightly smaller size posteriorly.

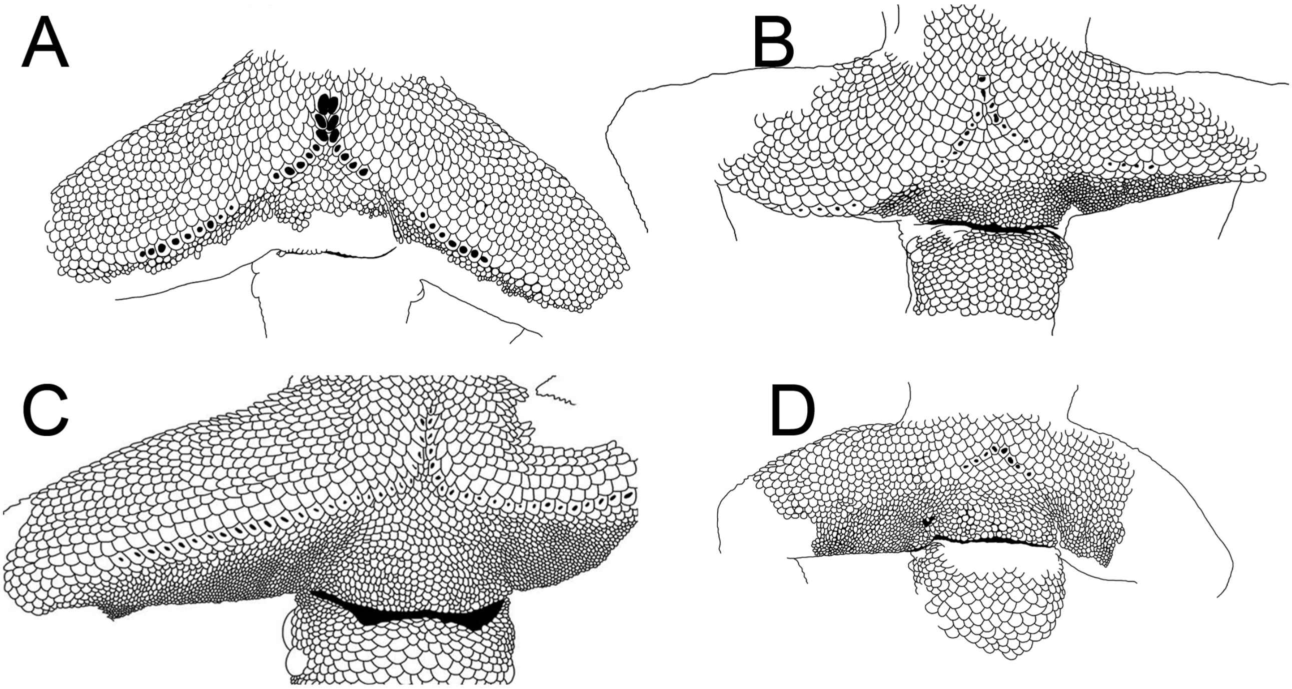

FIGURE 5. Precloacal depression and enlarged femoral and precloacal scales of members of the Javenese *marmoratus* complex. (A) *Cyrtodactylus mendol* **sp. nov**. holotype MZBLace 15007, (B) *C. belanegara* holotype MZBLace 15630, (C) *C. marmoratus* lectotype RMNH.RENA.2710a, (D) *Cyrtodactylus semiadii* voucher specimen MZBLace 15640. Illustrations by A. Riyanto and AAT Amarasinghe (not to scale).

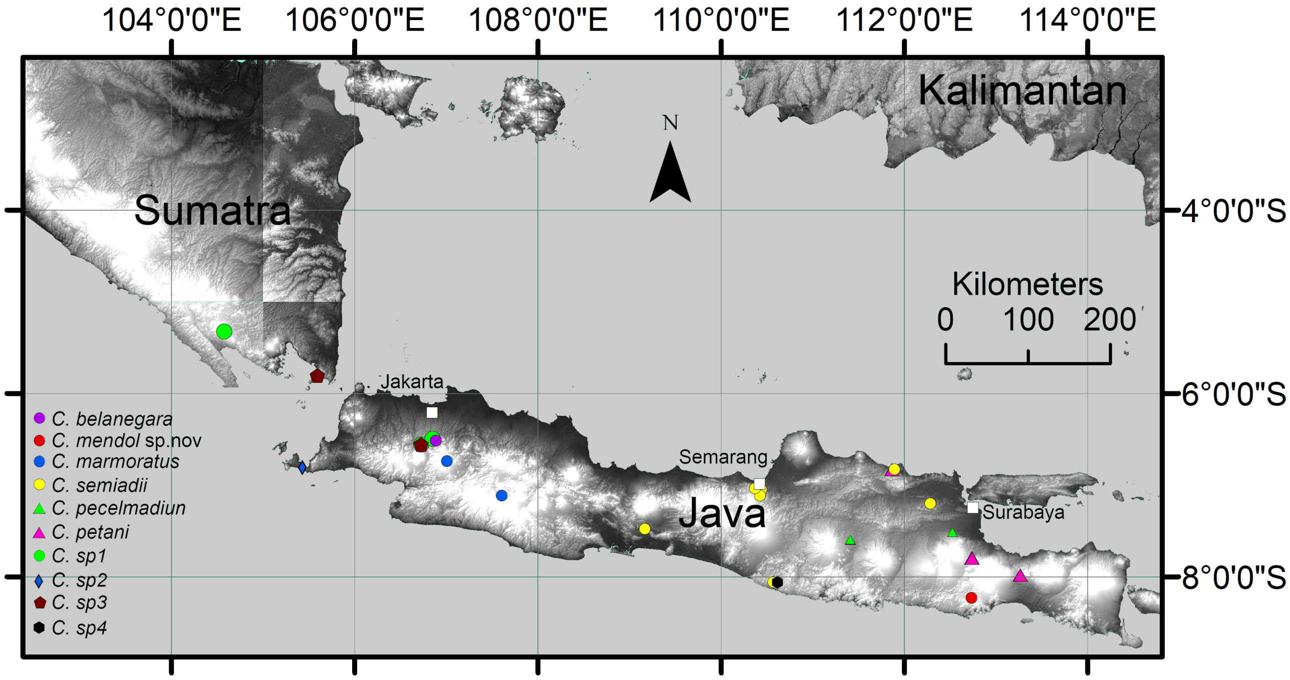

FIGURE 6. Map of Java illustrating the distribution of the Javanese *Cyrtodactylus darmanvillei* complex and the *C. marmoratus* complex.

Body elongate (AGL/SVL 0.42); dorsal scales small and granular, interspersed with relatively high, keeled to rounded tubercles irregularly arranged in 17 longitudinal rows at midbody; 30 paravertebral tubercles; ventrolateral body folds without tubercles. Ventral scales larger than dorsal scales, smooth, flat, imbricate, 39 ventral scale rows between ventrolateral body folds across the belly; enlarged scales immediately anterior to the cloacal opening absent.

Forelimbs relatively short (ForL/SVL 0.14); dorsal scales on forelimbs and upper arms smooth, forelimbs bearing tubercles, upper arm lacking tubercles; palmar scales flat, smooth, subimbricate; digits well developed, inflected at basal interphalangeal joints, digits slightly narrower distal to inflection; subdigital lamellae transversely expanded along the entire length of each digit, but slightly compressed in both length and width immediately distal to interphalangeal inflection; subdigital lamellae on digits of manus: F_1(14), F_2(16), F_3(15), F_4(16), F_5(16); claws well developed, sheathed by 2 dorsal scales and 1 ventral scale.

FIGURE 7. Habitat at type locality of *C. mendol* **sp. nov.** in Polaman village, Dampit, East Java, Indonesia. Photographs by Muhammad A. Fauzi.

Hindlimbs longer than forelimbs (TibL/SVL 01.39); covered dorsally by granular scales interspersed with larger, keeled tubercles; anterior ventral scales of thigh rounded, smooth, flat, subimbricate to juxtaposed; enlarged femoral and precloacal scales arranged in a continuous series, the largest in femoral part; precloacal groove present; 15 precloacofemoral pores arranged in inverse Y-shape; nine femoral pores on the right, seven on the left; three poreless femoral scales separate precloacal and femoral pores on the right, five on the left (Figure 4B & 5A); ventral scales on tibia smooth, flat, subimbricate; plantar scales slightly raised; digits well developed, inflected at basal metapodial-phalangeal joints, digits slightly narrower distal to inflection; subdigital lamellae transversely expanded along the entire length of each digit, but slightly compressed in both length and width immediately distal to interphalangeal inflection; subdigital lamellae on digits of pes: T_1(12), T_2(15), T_3(18), T_4(19), T_5(16); claws well developed, sheathed by 2 dorsal scales and 1 ventral scale.

Tail regenerated, 59.4 mm length; on the original part segmented, dorsally with keeled tubercles arranged in transverse rows forming whorls and original part of subcaudal without enlarged transverse plates; two postcloacal tubercles (spur) on each side in both sexes.

Coloration in life. Dorsal ground coloration overlain bright brown, ventral coloration is whitish pale. The rostral and narial region is yellowish, labials are pale white with yellow spots. A black stripe extending from the naris crossing the eyes to the tympanum. Dorsally, paired subcircular blotches cover the nape and extend to the original tail where they transform into irregularly shaped bands; five paired subcircular paravertebral blotches between axilla and groin, and two on the base of tail and three dark bands on the original tail; on the flanks thin blotches bordered by a thin yellow line occur between paired blotches, and several tubercles close to the ventrolateral body fold are bright yellow. The iris is goldish brown, edged in black and with black reticulum. Pupil vertical and black, overlaid with lighter brown than iris.

Variation. Detailed variation of mensural and meristic characters of the type series is presented in Table 4.

FIGURE 8. Mendol, a traditional food typically from Malang area, East Java, Indonesia. A. served on its own without other food. B. Served as a complementary side dish. Photographs by Richo Firmansyah.

TABLE 4. Meristic and morphometric data of the type series of *Cyrtodactylus mendol* **sp. nov.** NA=not applicable.

	Paratype	Holotype	Paratype	Paratype
MZBLace	15006	15007	15009	15010
Field Number	DP001	DP002	DP003	DP004
Sex	Male	Male	Female	Female
SVL (mm)	63.0	65.9	64.3	61.0
TL (mm)	Broken, lost	59.4 (regenerated)	9.3 (regenerated)	7.2 (regenerated)
Precloacal pores	17	15	Absent	Absent
Postrostrals between nostrils	3	3	5	3
Scales separated 2nd post metals	7	5	7	7
Post cloacal tubercles (left)	2 (2)	2 (2)	2 (2)	2 (2)
Poreless femoral scales seperating precloacal and femoral pores (left)	5 (4)	3 (5)	NA	NA
Femoral pores (left)	10 (12)	9 (7)	NA	NA
Enlarged median subcaudal	Absent	Absent	Absent	Absent
Precloacal depression	Grooved	Grooved	No	No
Precloacal pores arrangement	Inverse Y shape	Inverse Y shape	NA	NA
Abrupt transition	Present	Present	Present	Present
T1	11	12	12	10
T2	14	15	15	14
T3	18	18	18	17
T4	20	19	18	19
T5	17	16	16	18
DorT	18	17	18	18
PVT	33	30	35	35
VS	38	39	40	40
AGL	25.1	25.1	25.1	25.1
HL	17.1	17.1	17.1	17.1
SL	6.4	6.4	6.4	6.4
HH	6.6	6.6	6.6	6.6
HW	11.1	11.1	11.1	11.1
EE	4.9	4.9	4.9	4.9
ED	3.7	3.7	3.7	3.7
ArmL	8.7	8.7	8.7	8.7
TibL	11.0	11.0	11.0	11.0

TABLE 5. Selected morphological, morphometric, and meristic characters to diagnose *Cyrtodactylus mendol* **sp. nov.** and other Javanese recognized species; NA=not applicable, Specimens examined listed in Appendix 2.

	marmoratus complex				*darmandvillei* complex	
	mendol **sp. nov** (n=4)	*belanegara* (n=7)	*marmoratus* (n=7)	*semiadii* (n=10)	*pecelmadiun* (n=9)	*petani* (n=12)
Maximum SVL	65.9	53.8	85.7	51.4	67.2	69
Tubercles on occiput	Present	Present	Present	Present	Present	Present
Upper arm tubercles	Absent	Absent	Absent	Absent	Absent	
Ventrolateral body fold tubercles	Present	Present	Absent	Absent	Absent	Absent
Abrupt transition	Present	Present	Present	Absent	Present	Present
Precloacal depression	Present	Present	Present	Present	Present	Present
Precloacal pores arrangement	inverted Y-shape	inverted Y-shape	inverted Y-shape	inverted V-shape	inverted V-shape	inverted Y-shape
Enlarged transverse median subcaudal	Absent	Absent	Absent	Absent	Absent	Absent
Dorsal pattern	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched
Postrostrals between nostrils	3–5	5	5–9	5–7	3–4	3–4
Dorsal tubercles rows	17–18	18–20	11–19	18	18–20	15–20
Paravertebral tubercles	30–35	27–32	22–29	26–49	26–28	26–33
Ventral scales	38–40	37–40	34–46	34–45	28–34	32–40
Toe 4 lamellae	18–20	18–20	17–23	16–20	16–19	16–20
Enlarged precloacofemoral scale rows	2	1,2	2,3	no	2	3
Precloacofemoral pores	NA	NA	24–52	NA	32–37	30–40
Precloacal pores	15–16	12–13	NA	NA	NA	NA
Femoral pores (left)	9–10(7–12)	2–4(3–4)	NA	absent	NA	NA
Poreless femoral scales seperating precloacal and femoral pores (left)	3–5(4–5)	6–7(5–7)	Absent	NA	Absent	Absent
Post cloacal tubercles (left)	2(2)	2–3(1–3)	2(2)	2–4(3–4)	2–3(2–3)	2–3(2–3)
Scales betwen post mentals	5–7	5–8	5–6	4–6	3–4	3–4

Comparison. *Cyrtodactylus mendol* **sp. nov.** differs statistically ($p < 0.05$) from *marmoratus* group species in Java in the morphometric characters (Table 1), and the comparisons illustrated in Figure 5. From *C. belanegara* it can be differentiated by larger adult body size in SVL (known maximum 65.9 mm *versus* 53.8 mm), more postrostrals between nostrils (5 *versus* 3), more precloacal pores (15–17 *versus* 12–13), and more femoral pores (7–12 *versus* 2–4). It differs from *C. marmoratus* in having a smaller adult body size in SVL (known maximum 65.9 mm *versus* 85.7 mm), the configuration of precloacal pores and femoral pores separated by poreless scales (*versus* precloacal pores and femoral pores in a continuous arrangement). It differs from *C. semiadii* in having a larger adult body size in SVL (known maximum 65.9 mm *versus* 51.4 mm), femoral pores (*versus* a lacking), and an abrupt transition between large and small postfemoral scales and ventral femoral (*versus* gradual). It differs from both *darmandvillei* group species occurring in Java (*C. petani* and *C. pecelmadiun*) in discontinuous arrangement configuration between precloacal pores and femoral pores (*versus* continuous).

Distribution and natural history. *Cyrtodactylus mendol* **sp. nov.** at this time is recorded in Dampit, East Java (Figure 6). All specimens were collected from hillside limestone habitat with hilly topography at elevations ranging from 300 to 500 meters above sea level with sparse vegetation mixed with grasses, shrubs, and young trees (Figure 7). *Cyrtodactylus mendol* **sp. nov**. is nocturnal and is found in sympatry with *C. semiadii*.

Etymology. The specific epithet is a noun in apposition, "*mendol*." Mendol (Figure 8) is a traditional food typical of Malang (East Java) and its surrounding areas, known for its delicious taste and unique history. This dish is believed to be inspired by the popular Dutch food, mashed potato fritters. During the colonial era, Malang was one of areas where the Dutch resided. The term "*mendol*" means ball, which describes the method of forming the food into a ball shape. This dish is made from tempeh that has undergone further fermentation. The tempeh (fermented soybean cake) is crushed and mixed with spices such as garlic, coriander, galangal, lime leaves, and chili. The tempeh dough is then shaped into an oval form and fried until golden brown. Mendol has a savory taste with a hint of spiciness and a texture that is crispy on the outside but soft on the inside. It is typically served as a side dish for meals such as rawon, lodeh, and pecel.

Discussion

Both the *Cyrtodactylus marmoratus* and *C. darmandvillei* groups occurring in Java now have clearer and more comprehensible taxonomic statuses due to being studied using integrative taxonomy approaches with adequate samples from a broader range of localities. This is evidenced by the description of new species in 2024 (*C. belanegara*) and in 2025 (*C. pecelmadiun*). Four additional lineages, *C.* sp. 1 to *C.* sp. 4 (Fig. 3), await formal descriptions. We emphasize here that the body size as well as the presence and formation of precloacal and femoral pores are key factors for species-level identification in the *marmoratus* group.

Regarding dispersal and diversification in the *marmoratus* group, O'Connell *et al.* (2019) hypothesized two possible scenarios: first, the dispersal and diversification moved from west to east from the Thai-Malay Peninsula, to west Java (*C. marmoratus* and *C.* sp. 1, *C.* sp. 2, and *C.* sp. 3), and subsequently to New Guinea (*C. papuensis*); second, that *Cyrtodactylus* instead invaded west Java from unsampled ancestors on Borneo, which was connected to west Java during this time, but that intervening species have either gone extinct, or have not yet been sampled. We agree with O'Connell *et al.* (2019) that extinction and incomplete taxon sampling can strongly bias estimates of ancestral ranges, and as such, discovering additional extant species from this clade may help to resolve the diversification history of the *marmoratus* group

Therefore, identifying additional extant species within this clade could aid in clarifying the diversification history of the *marmoratus* group.

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Author Contributions

AR conceived and designed the study, conducted fieldwork and molecular work, performed data analyses, prepared figures and tables, and wrote the manuscript. AH, AA, RL, and FF contributed to the study design and manuscript writing. MM conducted molecular work. IS and ENS analyzed the data and wrote the manuscript. AMK, RF, and MAF conducted fieldwork, analyzed the data, prepared figures and tables, and wrote the manuscript. All authors reviewed and approved the final version of the manuscript.

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APPENDIX 1. Species included in our phylogenetic analysis with reference numbers and localities.

Species	Voucher	Locality	GenBank Acc	References
C. mendol **sp. nov**	MZBLace15006	Indonesia: East Java, Dampit	PV550415	This study
C. mendol **sp. nov**	MZBLace15007	Indonesia: East Java, Dampit	PV550416	This study
C. mendol **sp. nov**	MZBLace15010	Indonesia: East Java, Dampit	PV550417	This study
C. mendol **sp. nov**	MZBLace15009	Indonesia: East Java, Dampit	PV550418	This study
C. agusanensis	KU:320009	Mindanao Is	HQ154529	Welton *et al.* 2010b
C. agusanensis	KU 320015	Mindanao Is	HQ154531	Welton *et al.* 2010b
C. agusanensis	KU 320008	Mindanao Is	HQ154528	Welton *et al.* 2010b
C. astrum	LSUHC8815	Malaysia: Perlis, Kuala Perlis	JX519482	Grismer *et al.* 2012
C. astrum	LSUHC8809	Malaysia: Perlis, Gua Kelam	JX519480	Grismer *et al.* 2012
C. astrum	LSUHC8806	Malaysia: Perlis, Gua Kelam	JX519481	Grismer *et al.* 2012
C. australotitiwangsaensis	LSUHC8086	Malaysia: Perak, Fraser's Hill	JX519486	Grismer *et al.* 2012
C. australotitiwangsaensi	LSUHC8087	Malaysia: Perak, Fraser's Hill	JX519485	Grismer *et al.* 2012
C. australotitiwangsaensi	LSUHC6637	Malaysia: Pahang, Genting Highland	JX519484	Grismer *et al.* 2012
C. cf. agamensis	ENS19636	Indonesia; Sumatra, Agam	MH248910	O'Connell *et al.* 2019
C. cf. agamensis	ENS19635	Indonesia; Sumatra, Agam	MH248009	O'Connell *et al.* 2019
C. awalriyantoi	UNP163	Indonesia: West Sumatra, Padang Pariaman	OR122989	Ahda *et al.* 2023
C. awalriyantoi	UNP154	Indonesia: West Sumatra, Padang Pariaman	OR122990	Ahda *et al.* 2023
C. batucolus	LSUHC8934	Malaysia: Melaka, Pulau Besar	JQ889179	Johson *et al.* 2012
C. batucolus	LSUHC8933	Malaysia: Melaka, Pulau Besar	JQ889178	Johson *et al.* 2012

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APPENDIX 1. (Continued)

Species	Voucher	Locality	GenBank Acc	References
C. belanegara	MZBLace15630	Indonesia: Java Island, West Java, Sentul	PV453750	Riyanto *et al.* 2024a
C. belanegara	MZBLace15631	Indonesia: Java Island, West Java, Sentul	PV453751	Riyanto *et al.* 2024a
C. bintangrendah	LSUHC14351	Malaysia: Kedah, Tok Baling Cave	MN125083	Quah *et al.* 2019
C. bintangrendah	LSUHC14350	Malaysia: Kedah, Tok Baling Cave	MN125082	Quah *et al.* 2019
C. bintangtinggi	LSUHC9006	Malaysia: Perak, Bukit Larut	JX519494	Grismer *et al.* 2012
C. bintangtinggi	LSUHC8862	Malaysia: Perak, Bukit Larut	JX519493	Grismer *et al.* 2012
C. consobrinus	CAS262851	Malaysia: Serawak	MK477181	Davis *et al.* 2019
C. consobrinus	CAS262853	Malaysia: Serawak	MK477184	Davis *et al.* 2019
C. consobrinus	CAS262854	Malaysia: Serawak	MK477183	Davis *et al.* 2019
C. consobrinus	CAS262852	Malaysia: Serawak	MK477182	
C. darmandvillei	WAMR98393	Indonesia: Sumbawa Besar	JX440533	Wood *et al.* 2012
C. equestris	AMSR135520	PNG	KT835458	Oliver *et al.* 2016
C. equestris	AMSR119547	PNG	KT835457	Oliver *et al.* 2016
C. gonjong	UNP062	Indonesia: West Sumatra, Padang Pariaman	OR208785	Nugraha *et al.* 2023
C. gonjong	UNP045	Indonesia: West Sumatra, Padang Pariaman	OR208786	Nugraha *et al.* 2023
C. gonjong	UNP146	Indonesia: West Sumatra, Padang Pariaman	OR208781	Nugraha *et al.* 2023
C. guakanthanensis	LSUHC11323	Malaysia: Perak, Gua Kanthan	KU253577	Grismer *et al.* 2016
C. guakanthanensis	LSUHC11322	Malaysia: Perak, Gua Kanthan	KU253576	Grismer *et al.* 2016
C. gunungsenyumensis	LSUHC12204	Malaysia: Pahang, Gunung Senyum	KU253586	Grismer *et al.* 2016
C. gunungsenyumensis	LSUHC12205	Malaysia: Pahang, Gunung Senyum	KU253584	Grismer *et al.* 2016
C. gunungsenyumensis	LSUHC12201	Malaysia: Pahang, Gunung Senyum	KU253585	Grismer *et al.* 2016
C. hantu	BRK436	Malaysia: Serawak	MN884174	Davis *et al.* 2020
C. hantu	BRK442	Malaysia: Serawak	MN884173	Davis *et al.* 2020
C. hantu	BRK437	Malaysia: Serawak	MN884175	Davis *et al.* 2020
C. hutan	UNIMAS9644	Malaysia: Serawak	OP480051	Davis *et al.* 2023
C. hutan	UNIMAS9645	Malaysia: Serawak	OP480052	Davis *et al.* 2023
C. hutan	UNIMAS9649	Malaysia: Serawak	OP480053	Davis *et al.* 2023

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APPENDIX 1. (Continued)

Species	**Voucher**	**Locality**	**GenBank Acc**	**References**
C. jambangan	KU314806	Philippine: Mindano Is	GU366101	Welton *et al.* 2010a
C. jambangan	KU314793	Philippine: Mindano Is	GU366100	Welton *et al.* 2010a
C. jambangan	KU314835	Philippine: Mindano Is	GU366099	Welton *et al.* 2010a
C. jellesmae	RMB1692	Indonesia: Sulawesi	GU550720	Siler *et al.* 2010
C. jellesmae	RMB1672	Indonesia: Sulawesi	GU550721	Siler *et al.* 2010
C. jatnai	MVZ274340	Indonesia: Bali Is.	OP356366	Reilly *et al.* 2023
C. jatnai	MVZ274344	Indonesia: Bali Is.	OP356365	Reilly *et al.* 2023
C. limajalur	CAS262848	Malaysia: Serawak	MK477178	Davis *et al.* 2019
C. limajalur	CAS262846	Malaysia: Serawak	MN884124	Davis *et al.* 2019
C. marmoratus	ABTC48075	Indonesia: West Java, Cibodas	JQ820292	Oliver *et al.* 2012
C. marmoratus	ENS15932	Indonesia: West Java, Cibodas	KR921721	Harvey *et al.* 2015
C. marmoratus	MUN1027	Indonesia: West Java, Gunung Puntang	PV983426	Riyanto *et al.* 2024a
C. metropolis	LSUHC11343	Malaysia: Selangor, Batu Caves	KU253578	Grismer *et al.* 2014
C. miriensis	BRK579	Malaysia: Serawak, Lambir	MN884155	Davis *et al.* 2021
C. miriensis	BRK572	Malaysia: Serawak, Lambir	MN884154	Davis *et al.* 2021
C. miriensis	BRK721	Malaysia: Serawak, Lawas	MN884153	Davis *et al.* 2021
C. muluensis	CAS262984	Malaysia: Serawak, Mulu	MK477170	Davis *et al.* 2019
C. muluensis	CAS262985	Malaysia: Serawak, Mulu	MK477163	Davis *et al.* 2019
C. muluensis	CAS262983	Malaysia: Serawak, Mulu	MK477169	Davis *et al.* 2019
C. novaeguineae	SAMAR62648	PNG	JQ820302	Oliver *et al.* 2012
C. novaeguineae	AMSR122410	PNG	JQ820301	Oliver *et al.* 2012
C. payacola	LSUHC9982	Malaysia: Penang, Bukit Panchor	JQ889192	Johson *et al.* 2012
C. payacola	LSUHC10070	Malaysia: Penang, Bukit Panchor	JQ889190	Johson *et al.* 2012
C. payacola	LSUHC10071	Malaysia: Penang, Bukit Panchor	JQ889191	Johson *et al.* 2012
C. papeda	MZBLace14052	Indonesia: Obi Is.	OM158779	Riyanto *et al.* 2022
C. papuensis	PMO3	PNG	OM517150	Tallowin *et al.* 2018
C. papuensis	SAMAR62651	PNG	JQ820321	Oliver *et al.* 2012
C. papuensis	SAMAR62652	PNG	JQ820320	Oliver *et al.* 2012
C. papuensis	AA1914	Indonesia: Fakfak	OM517149	Tallowin et al. 2018
C.cf. papuensis	JAM2242	Indonesia: Buru Is.	MF169967	Brennan *et al.* 2017
C.cf. papuensis	TNHC59549	Indonesia: Buru Is.	JX440546	Wood *et al.* 2012
C.cf. papuensis	MZBLace.5419	Indonesia: Rajampat Is.	JQ820315	Oliver *et al.* 2012

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APPENDIX 1. (Continued)

Species	**Voucher**	**Locality**	**GenBank Acc**	**References**
C. pecelmadiun	MZBLace15691	Indonesia: East Java, Mojokerto	PQ591471	Riyanto *et al.* 2025
C. pecelmadiun	MZBLace15690	Indonesia: East Java, Mojokerto	PQ591470	Riyanto *et al.* 2025
C. pecelmadiun	MZBLace15692	Indonesia: East Java, Maospati	PQ591469	Riyanto *et al.* 2025
C. pecelmadiun	MZBLace15689	Indonesia: East Java, Maospati	PQ591468	Riyanto *et al.* 2025
C. petani	MZBLace15000	Indonesia: East Java, Lumajang, Klakah	MT704864	Riyanto *et al.* 2020
C. petani	MZBLace15001	Indonesia: East Java, Lumajang, Klakah	MT704865	Riyanto *et al.* 2020
C. petani	MZBLace11706	Indonesia: East Java, Pasuruan	KU232620	Riyanto *et al.* 2015
C. petani	MZBLace12899	Indonesia: East Java, Pasuruan	KU232619	Riyanto *et al.* 2015
C. phippinicus	FMNH236073	Philippines, Romblon Island	JX440550	Wood *et al*. 2012
C. psarops	MZBLace9687	Indonesia: Sumatra, Ngarip	MH248931	O'Connell *et al.* 2019
C. psarops	MZBLace9686	Indonesia: Sumatra, Ngarip	MH248930	O'Connell *et al.* 2019
C. psarops	UTA 61579	Indonesia: Sumatra, Ngarip	MH248927	O'Connell *et al.* 2019
C. pubisulcus	CAS262963	Malaysia: Serawak	MK477166	Davis *et al.* 2019
C. pubisulcus	CAS262964	Malaysia: Serawak	MK477165	Davis *et al.* 2019
C. quadrivirgatus	LSUHC9864	Malaysia: Perak, Bukit Larut	GU550736	Siler *et al.* 2010
C. quadrivirgatus	LSUHC10072	Malaysia: Penang, Bukit Pancor	JQ889193	Johson *et al.* 2012
C. redimiculatus	KU309327	Philippines: Palawan Is.	GU550743	Siler *et al.* 2010
C. redimiculatus	KU309328	Philippines: Palawan Is.	GU550742	Siler *et al.* 2010
C. redimiculatus	KU309326	Philippines: Palawan Is.	GU550744	Siler *et al.* 2010
C. rex	SAMAR67636	PNG	KT835461	Oliver *et al.* 2016
C. rex	SAMAR67637	PNG	KT835460	Oliver *et al.* 2016
C. rex	BPBM18655	PNG	KT835463	Oliver *et al.* 2016
C. rosichonarieforum	MZBLace12132	Indonesia: Bunguran Is.	KP256187	Riyanto *et al.* 2015
C. sadleiri	SAMAR34810	Chrismas Is.	JQ820309	Oliver *et al.* 2012
C. semenanjungensis	LSUHC8900	Malaysia: Johor, Gunung Panti	JQ889177	Johson *et al.* 2012
C. semiadii	MZBLace14818	Indonesia: Java, Yogjakarta	MT704866	Riyanto *et al.* 2020
C. semiadii	MZBLace14580	Java: Tembalang, Semarang	PV999954	Riyanto *et al.* 2024b

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APPENDIX 1. (Continued)

Species	**Voucher**	**Locality**	**GenBank Acc**	**References**
C. semiadii	MZBLace14581	Java: Tembalang, Semarang	PV999955	Riyanto *et al.* 2024b
C. semicinctus	ENS14966	Indonesia: Sumatra, Kerinci	MH248924	Harvey *et al.* 2015
C. semicinctus	UTA 61588	Indonesia: Sumatra, Kerinci	MH248923	Harvey *et al.* 2015
C. semicinctus	ENS 14749	Indonesia: Sumatra, Kerinci	MH248925	Harvey *et al.* 2015
C. seribuatensis	LSUHC6348	Malaysia: Johor, Pulau Mentigi	JX440557	Wood *et al.* 2012
C. seribuatensis	LSUHC6349	Malaysia: Johor, Pulau Mentigi	MF169976	Brennan *et al.* 2017
C. seribuatensis	LSUHC6349	Malaysia: Johor, Pulau Nangka Kecil	JQ889187	Johson *et al.* 2012
C. cf. serratus	SAMAR62635	PNG	JQ820297	Oliver *et al.* 2012
C. sermowaiensis	BPBM23317	PNG	JX440558	Wood *et al.* 2012
C. sworderi	LSUHC7685	Malaysia: Johor, Endau-Rompin, Peta, Sungai Kawal	JQ889189	Johson *et al.* 2012
C. tautbatorum	KU309319	Malaysia: Palawan Is.	GU366083	Siler *et al*. 2010
C. tautbatorum	KU309321	Malaysia: Palawan Is.	GU366081	Siler *et al*. 2010
C. tautbatorum	KU309320	Malaysia: Palawan Is.	GU366082	Siler *et al*. 2010
C. tebuensis	LSUHC10903	Malaysia: Terengganu, Gunung Tebu	JX988528	Grismer *et al.* 2013
C. tebuensis	LSUHC10902	Malaysia: Terengganu, Gunung Tebu	JX988527	Grismer *et al.* 2013
C. tebuensis	LSUHC10852	Malaysia: Terengganu, Gunung Tebu	JX988525	Grismer *et al.* 2013
C. tehetehe	MZBLace15614	Indonesia: Maratua Is.	PP092503	Wiradarma *et al.* 2024
C. tehetehe	MZBLace15613	Indonesia: Maratua Is.	PP092502	Wiradarma *et al.* 2024
C. zugi	MZBLace5575	Indonesia: Maratua Is.	JQ820306	Oliver *et al.* 2012
C. zugi	MZBLace5573	Indonesia: Batanta Is.	JQ820305	Oliver *et al.* 2012
C. sp. 1	ENS15759	Indonesia: Java, Bogor	MH248933	Harvey *et al.* 2015
C. sp. 1	ENS15784	Indonesia: Java, Bogor	KR921689	Harvey *et al.* 2015
C. sp. 1	ENS14124	Indonesia: Sumatra, Ngarip	MH248932	Harvey *et al.* 2015
C. sp. 2	ENS15813	Indonesia: Java, Bogor	MH248940	O'Connell *et al.* 2019
C. sp. 2	ENS13751	Indonesia: Sumatra, Lampung	MH248942	O'Connell et al. 2019
C. sp. 3	HLM0371	Indonesia: Java, Ujung Kulon	MW792056	O'Connell *et al.* 2019
C. sp. 4	TR094	Java: Yogjakarta, Tanjungsari	TR094	Riyanto *et al.* 2024a

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APPENDIX 1. (Continued)

Species	Voucher	Locality	GenBank Acc	References
Gekko gecko	MVZ215314	Thailand: Patong Beach, Kathu District, Phuket Island, Phuket Province	AF114249	Macey *et al. 1999*
Hemidactylus frenatus	LSUHC4871	Malaysia: Pahang, Bukit Bakong	GQ458049	Bauer *et al*. 2010

Appendix 2. Comparative material examined

Cyrtodactylus belanegara. MZB. Lace. 15631, 15634, 15635, 15636, adult males; MZB.Lace. 15630, 15632, 15633, adult females, Sentul, West Java, Indonesia.

Cyrtodactylus jatnai. MZB. Lace. 8726, 8729, 8731, UIMZ. 0081-82, UIMZ. 0101, adult males, MZBLace 8725, 8728, adult females, Teluk Menjangan, Bali, Indonesia.

Cyrtodactylus marmoratus. MZBLace 9709, 15701, adult males, 9706-08, 9710-11, adult females, Cibodas, West Java, Indonesia.

Cyrtodactylus pecelmadiun. MZB. Lace. 15689, 15693-97, adult males, Maospati; MZB, Lace. 15690, adult males, Mojosari; MZB. Lace. 15691, female, Mojosari; MZB. Lace. 15692, female, Maospati, East Java, Indonesia.

Cyrtodactylus petanii. MZB.Lace. 15000-01, adult males, Lumajang, East Java; MZB.Lace. 11706, 11708-10, 11712-13, 12143, 12899, adult males, Pasuruan; MZB. Lace. 11707, 11711, adult females, Pasuruan, East Java, Indonesia.

Cyrtodactylus semiadii. MZB.Lace. 9104, adult male, Tuban, East Java; MZB. Lace. 10827, adult female, Bantul, Yogjakarta; MZB. Lace. 15670-71, Patikraja, Central Java; MZB. Lace. 15672, Penggaron, Central Java; 15673-75, Gunung Pati, Central Java; MZB. Lace. 15676-77, Lamongan, East Java, Indonesia.